# Why the long face? Static allometry in the sexually dimorphic phenotypes of Neotropical electric fishes

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The evolution of sexually dimorphic traits is thought to have marked effects on underlying patterns of static allometry. These traits can negatively affect organismal survivability by creating trade-offs between trait size and performance. Here we use three-dimensional geometric morphometrics to study the static allometry of two species of sexually dimorphic electric fishes (*Apteronotus rostratus* and *Compsaraia samueli*) in which mature males grow elongate jaws used in agonistic male–male interactions. We also estimate jaw-closing performance between the sexes of both species to track changes in kinematic transmission associated with the development of sexual weaponry. We find significantly different patterns of static allometry between the sexes of both species, with males exhibiting more positive allometric slopes relative to females. We also find a negative relationship between skull shape and mandibular kinematic transmission in *C. samueli*, suggesting a trade-off where males with longer faces exhibit lower mechanical advantages, suggesting weaker jaw leverage. In contrast, males and females of *A. rostratus* exhibit no difference between sexes in mechanical advantage associated with facial elongation.

ADDITIONAL KEYWORDS: biomechanics – geometric morphometrics – gymnotiformes – sexual dimorphism – sexual selection.

## INTRODUCTION

Sexually selected traits used as weapons in competition for resources, and ultimately access to mates, have evolved multiple times across the tree of life, and have produced a diversity of elaborate phenotypes ranging from the enlarged mandibles and horns of stag beetles (Scarabaeoidea: Lucanidae), to the elongate jaws or kypes in some male salmon species (Salmoniformes: Salmonidae) (Quinn & Foote, 1994; Crespi & Teo, 2002; Kawano, 2006; Emlen *et al.*, 2012). These weapons are often used to defend resources and settle conflicts between individuals through combat or display, and may also serve as an honest signal to potential mates about viability (Berglund *et al.*, 1996; Emlen, 2008). Sexual weaponry may also result in deleterious effects on performance or reduced survivorship, such

that trade-offs between the size of a weapon and survivorship may ultimately limit the range of phenotypic disparity (Zahavi, 1975; Stearns, 1989; Schluter *et al.*, 1991; Petrie, 1992; Gustafsson *et al.*, 1995). These trade-offs can also have marked effects on the underlying static allometries that build sexual weapons, such that differences in viability associated with increases in trait or body size can influence the static allometric slope of a trait (Bonduriansky & Day, 2003).

Static allometry refers to the log–log relationship between the size and shape of traits and body size across individuals at the same developmental stage (Cheverud, 1982; Pélabon *et al.*, 2013). The evolutionary mechanisms underlying static allometry within and among species, and the consequences of these mechanisms on trait shapes and related functions, have been extensively discussed (Gould, 1966; Emerson & Bramble, 1993; Bonduriansky, 2007; Eberhard, 2009; Pélabon *et al.*, 2014). Dimorphism in sexual traits is thought to influence the evolution of

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static allometry, with studies hypothesizing that traits under sexual selection should exhibit positive allometric slopes relative to traits that are not under sexual selection (Darwin, 1888; Petrie, 1988; Emlen & Nijhout, 2000; Emlen *et al.*, 2005). Positive allometry in sexually dimorphic traits may arise when larger trait sizes confer direct advantages in sexual competition (Green, 1992). More recent studies documenting sexual dimorphism across a wide array of taxa have found a diversity of patterns in static allometry underlying sexually selected traits. These studies have hypothesized that the function of sexually selected traits, and the life history of the organisms that possess them, may influence the evolution of their static allometry (Bonduriansky & Day, 2003; Bonduriansky, 2007).

## STUDY SYSTEM

Apteronotid electric fishes (Apteronotidae: Gymnotiformes) represent an excellent case for the study of sexual dimorphism. In this clade, fishes exhibit a wide diversity of skull shapes ranging from highly foreshortened to highly elongate skulls, with each phenotype evolving multiple times independently (Evans et al., 2017b, c). Amongst this diversity in skull shapes, an interesting pattern of sexual dimorphism has emerged: in some species, mature males grow elongate snouts and oral jaws for use in agonistic interactions (jaw-locking behaviours and aggressive displays) with conspecific males (Triefenbach & Zakon, 2008; Albert & Crampton, 2009) (Fig. 1). This particular form of sexual dimorphism is thought to have evolved multiple times independently within the family (Py-Daniel & Fernandes, 2005; Hilton & Cox-Fernandes, 2006; Albert & Crampton, 2009; Fernandes *et al.*, 2009a; Tagliacollo *et al.*, 2016). The developmental mechanisms that underlie growth of elongate snout and jaw phenotypes are less well-known, and appear to vary among gymnotiform species (Petzold & Smith, 2016). In some cases, sexual dimorphism is so pronounced that the sexes were initially classified as different species (Cox-Fernandes *et al.*, 2009; Fernandes *et al.*, 2009b).

Facial elongation in electric fishes also presents an interesting system for the study of sexual weaponry. From a functional perspective, the typical teleost jaw is an integrated system of levers and linkages that controls the opening and closing of the jaws in feeding and other activities (Westneat, 2003, 2004). There is an extensive literature that documents the biomechanical effects of changes in jaw-lever lengths, and the resulting functional consequences for kinematic transmission (Grubich, 2005; Hulsey *et al.*, 2005; Martinez & Sparks, 2017). The elongation of the snout and oral jaws in sexually dimorphic electric fishes may,

therefore, result in changes in the kinematic transmission of the jaws, as the relative lengths of jaw levers may vary ontogenetically between the sexes. These changes in kinematic transmission may pose a trade-off between jaw-closing performance and the rostral length of an organism. Here, we explicitly define the term 'trade-off' as a negative residual correlation between a morphological and physiological variable, following the definition from Holzman *et al.* (2012).

Here we use three-dimensional geometric morphometrics to study the evolution of static allometry in sexually dimorphic phenotypes for two species of apteronotid electric fishes: *Apteronotus rostratus* and *Compsaraia samueli*, both of which have been reported to exhibit aggressive jaw-locking behaviour between mature males (Triefenbach & Zakon, 2008; Albert & Crampton, 2009), and track allometric changes in kinematic transmission of the mandible between the sexes in each species. We hypothesize that the sexually dimorphic males of each species will exhibit differential patterns of allometry relative to conspecific females and that males will differ significantly from females in kinematic transmission of their respective mandibles as a result of their facial elongation.

## MATERIAL AND METHODS

### ANCESTRAL STATE RECONSTRUCTION

The ancestral state of sexually dimorphic craniofacial elongation was reconstructed for 93 species of Apteronotidae using the Bayesian approach of stochastic character mapping [*sensu* Bollback (2006) in the *R*-package: PHYTOOLS (Revell, 2012)]. Character history was modelled as a discrete trait under an 'equal rates' transition matrix model using the Tagliacollo *et al.* (2016) phylogeny, pruned in the r-package APE (Paradis *et al.*, 2004) to include only the 93 apteronotid taxa. Transition frequencies of ancestral states were estimated from 1000 simulations and plotted at each node of the phylogeny. Sexually dimorphic data were gathered from the literature for all available apteronotid species. We considered the sexually dimorphic pattern of *Sternarchogiton nattereri* (where males grow robust dentition from their upper and lower jaws) as a form of craniofacial elongation because the skull and jaws also elongate in mature males, although to a lesser degree (Cox-Fernandes *et al.*, 2009).

### SPECIMEN SELECTION AND PREPARATION

*Apteronotus rostratus* and *C. samueli* are allopatric and occur in different habitats. As a result, collection methods differed dramatically between species in this study. *Apteronotus rostratus* is only known

**Figure 1.** CT scans of male and female *Compsaraia samueli* and *Apteronotus rostratus* specimens showing secondary sexually-dimorphic differences in cranial shapes. Note males (B, D) with more elongate facial phenotypes, and females (A, C) with relatively foreshortened facial phenotypes.

from Panama and Colombia where it inhabits small streams and fast-flowing creeks (Gogarten *et al.*, 2008; Santana & Vari, 2013). A total of 31 (12 male and 19 female) specimens were collected in the Chepo region of Panama during the dry season (December–March 2016) using dip nets aided by electric-fish finders to target individuals. To increase sample size, specimens collected in the field during this period were pooled with 26 museum specimens (five males, 21 females) from the Smithsonian Tropical Research Institute (STRI) collected from nearby (Supporting Information, Table S1).

*Compsaraia samueli* is endemic to the Amazon River basin where it inhabits deep river channels (Albert & Crampton, 2009; Bernt & Albert, 2017). A total of 49 (26 male and 23 female) specimens were collected from the area near Iquitos, Peru, during the high- and low-water periods (August 2015–January 2017) using purse seines pulled between two wooden canoes. Specimens of both species were dissected, and gonads inspected to determine sex. All specimens of both species were humanely euthanized using an overdose of MS-222, fixed in 10% unbuffered formalin for at least 48 h in a flat covered tray, washed in water twice for 24 h each, then transferred to 70% ethanol for long-time storage. All collected specimens were deposited at the Academy of Natural Sciences in Philadelphia (Supporting Information, Table S1).

The study of static allometry can be heavily influenced by geographic variation (Pélabon *et al.*, 2014; Voje *et al.*, 2014). Studies involving fishes can be particularly sensitive to these effects because they exhibit indeterminate growth that may be influenced by variation in local conditions (Evans *et al.*, 2017b). To reduce the effects of geographic variation, we limited our study to include only specimens of each species collected from localities separated by less than 15 km.

## MICRO-CT SCANNING

Specimens of *A. rostratus* and *C. samueli* are rare in museum collections. It was, therefore, unfeasible to clear and stain or otherwise dissect individuals, as this process permanently alters specimens (Taylor & Van Dyke, 1985). Instead, we used micro-CT scanning to capture the fine-scale osteological properties of individuals. This technique produced high-resolution images of the internal anatomy of specimens while leaving them unperturbed. For *A. rostratus*, a size series of 30 specimens (49–212 mm total length) was scanned at the University of Texas, Austin (UT), using a custom-built scanner by North Star Imaging (NSI) at 180 kV, 114–115 µA and 19–49 µm voxel size. The remaining 27 specimens were scanned at the University of Washington Friday Harbor Labs (UW) Karl Liem Memorial Bio-Imaging Facility in conjunction with the 'ScanAllFishes' project using a Bruker Skyscan 1173 at 70 kV, 114 uA and 28.2 µm voxel size. For *C. samueli*, a size series of 49 specimens (67–194 mm total length) were scanned at (UW) at 65–70 kV, 114–123

**Table 1.** Landmark definitions for the three-dimensional geometric morphometric analysis of skull shape for *Apteronotus rostratus* and *Compsaraia samueli*

| Landmark # | Landmark description |
|---|---|
| 1 | Mesethmoid-anterior-most tip |
| 2 | Mesethmoid-ventral ethmoid-mesethmoid ventral margin |
| 3 | Ventral ethmoid-ventral ethmoid-parasphenoid margin |
| 4 | Ventral ethmoid-ventral ethmoid-mesethmoid dorsal margin |
| 5 | Frontal-mesethmoid-frontal margin |
| 6 | Orbitosphenoid-anterior-most orbitosphenoid-frontal margin |
| 7 | Orbitosphenoid-anterior-most orbitosphenoid-parasphenoid margin |
| 8 | Pterosphenoid-orbitosphenoid-pterosphenoid-frontal margin |
| 9 | Pterosphenoid-orbitosphenoid-pterosphenoid ventral margin |
| 10 | Parasphenoid-posterior -most orbitosphenoid-parasphenoid margin |
| 11 | Parasphenoid-pterosphenoid-parasphenoid margin |
| 12 | Parietal-lateral-most parietal-frontal suture |
| 13 | Prootic-prootic foramen |
| 14 | Supraoccipital-posterior-most projection of supraoccipital crest |
| 15 | Supraoccipital-exoccipital-supraoccipital margin |
| 16 | Basioccipital-posterior-ventral-most point of basioccipital |
| 17 | Basioccipital-posterior-most-parasphenoid-basiocciptal margin |
| 18 | Frontal-anterior-most segment of anterior fontanel |
| 19 | Frontal-posterior-most segment of anterior fontanel |
| 20 | Frontal-anterior-most segment of posterior fontanel |
| 21 | Parietal-posterior-most segment of anterior fontanel |
| 22 | Dentary-anterior-most tooth |
| 23 | Dentary-dorsal-most-dentary-angular-margin |
| 24 | Angular-centre of jaw joint |
| 25 | Retroarticular-posterior-ventral-most point on retroarticular |

uA, 24–35.7 μm voxel size, 1175–1200 ms exposure, and a CCD sensitivity of 2240 × 2240 pixels. All micro-CT scans of both species are freely available for download from Open Science Framework at: osf.io/m8tqe.

### THREE-DIMENSIONAL GEOMETRIC MORPHOMETRICS

To study the allometric shape changes of the skull between sexes of the two species, we used three-dimensional geometric morphometrics performed on isosurfaces rendered from micro-CT slice data. Image stacks were imported into Stratovan Checkpoint and converted to three-dimensional isosurfaces to capture the surface properties of the bone. The left side of each specimen was digitized with 25 landmarks (LM) and exported to MorphoJ (Klingenberg, 2011) for subsequent statistical analysis (Table 1; Fig. 2A–D).

### NEUROCRANIAL ALLOMETRIC TRAJECTORIES

To remove the effect of differential scaling and orientation in the shape data, a full Procrustes superimposition was performed in MorphoJ. Procrustes coordinates were then used to study the allometric relationship between skull shape and log-transformed centroid-size. Variation in allometric slopes between sexes was assessed in the R-package GEOMORPH (Adams & Otárola-Castillo, 2013) using the 'procD.allometry' function, which implements a Procrustes ANOVA to test against the null hypothesis of parallel or homogenous slopes between the sexes of the two
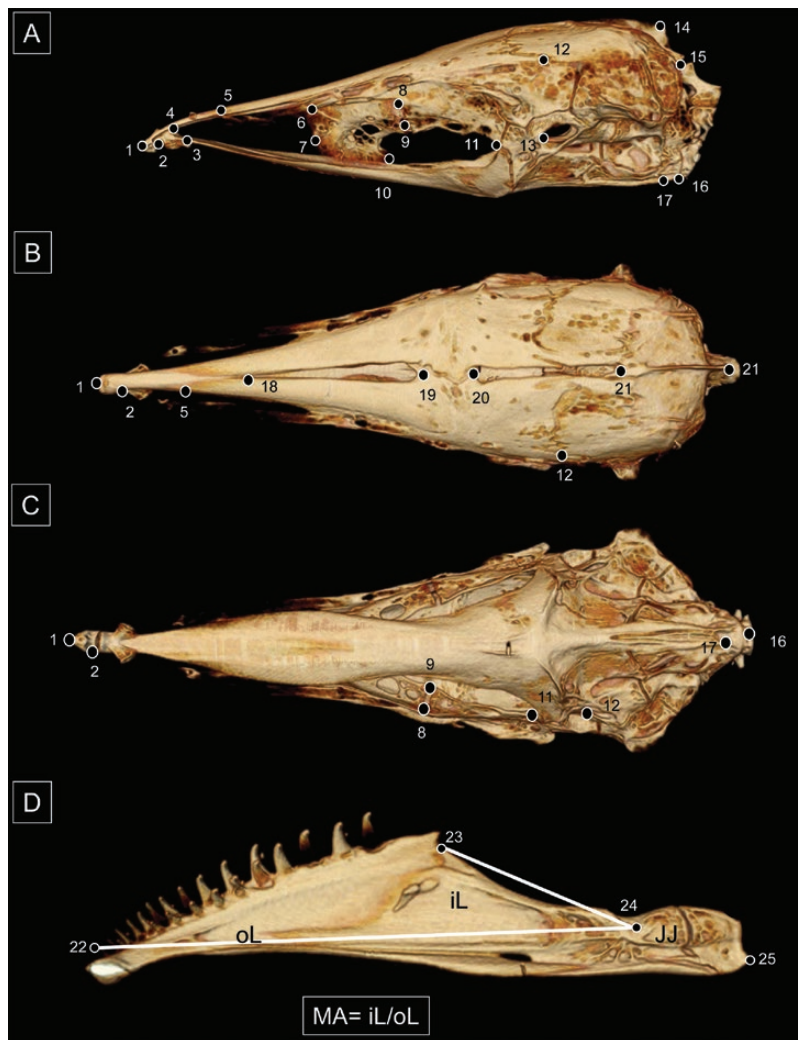


**Figure 2.** CT scans of *Apteronotus rostratus* (ANSP 200222) in lateral (A), dorsal (B), ventral (C) and mandibular (D) views showing 25 three-dimensional landmarks used for the geometric morphometric analysis of *Compsaraia samueli* and *Apteronotus rostratus* and in-lever (iL) and out-lever (oL) measurements taken from the jaw joint (JJ). Abbreviation: MA, mechanical advantage.

species. Allometric slopes are displayed using a predicted shape vs. log(centroid-size) regression and a common allometric component (CAC) vs. log(centroid-size) regression. A predicted shape regression calculates the predicted values of a regression of shape on size and plots the first principal component scores of the predicted values in the form of an allometric trend (Adams & Nistri, 2010). The CAC approach performs a pooled regression of shape variables corrected, in this case, for the different means between sexes of both species and estimates the average allometric trend within groups (Mitteroecker *et al.*, 2004). Here we quantify size as the log(centroid size) of skull shape. Electric fishes possess the ability to regenerate a significant portion of their bodies after being damaged by predation. As a result, total length is often a poor estimate of size; to correct for this, dimensions of head length are frequently utilized as a proxy for overall size (Albert, 2001; Bernt & Albert, 2017; Evans et al., 2017a, 2018).

### ESTIMATING PERFORMANCE OF THE MANDIBLE

During agonistic jaw-locking interactions in electric fishes, individuals typically bite the heads, flanks and tails of conspecifics. They may also interlock their jaws and push linearly or twist laterally upon making contact (depending on the species) (Triefenbach & Zakon, 2008; Albert & Crampton, 2009). Due to the importance of the closing action of the jaws during these bouts, we hypothesize that the relative jaw-closing performance of individuals is a major factor in determining the winner of aggressive interactions between rival males. To model this, we estimate the jaw-closing performance of the mandible using a simple model of kinematic transmission: closing mechanical advantage (MA). Closing mechanical advantage is quantified as the ratio between the closing in-lever distance (distance between the dorsal insertion of the A2 sub-unit of the adductor mandibulae muscle and the articulation of the jaw joint) and out-lever distance (distance between jaw joint and most anterior tooth) (Westneat, 2004), such that $MA = iL/oL$ (Fig. 2D).

Changes in MA can have dramatic effects on force transmission and relative velocity transfer, where higher mechanical advantages in the lower jaw correspond to greater force transmission, while lower mechanical advantages correspond to less forceful transmissions but faster jaw closing (Wainwright *et al.*, 1991; Westneat, 2003; Holzman *et al.*, 2012; Kolmann *et al.*, 2018). Here we study the allometric scaling of log-transformed MA with log-transformed centroid-size and lower jaw shape (LM 22–25; subset from the total landmark configuration) in male and female specimens of *A. rostratus* and *C. samueli* to test for differences in slopes between sexes in each species and identify potential trade-offs in kinematic transmission associated with jaw elongation.

### VIDEO RECORDINGS OF BEHAVIOUR

Agonistic interactions between *C. samueli* males were filmed at the 'Amazon Tropicals' aquarium store in Iquitos, Peru. Individuals were collected by aquarium fishermen and housed in 40-gallon aquaria, where they were subsequently filmed by the authors using a GoPro Hero 5 at 240 fps. Videos were rendered at 60 fps using Adobe Premier Pro Creative Cloud. Video recordings were not available for *A. rostratus* due to high mortality rates experienced shortly after capture for this species.

## RESULTS

### SEXUAL DIMORPHISM IN APTERONOTIDAE

Within Apteronotidae, the pattern of sexually dimorphic craniofacial elongation has evolved multiple times independently (Fig. 3). Stochastic character mapping reveals that this pattern evolved independently in *Parapteronotus*, twice independently in *Apteronotus*
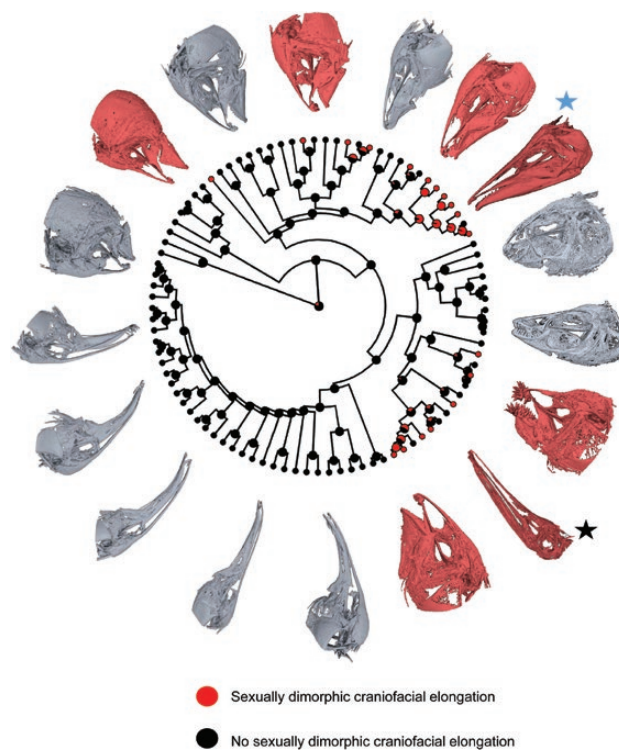


**Figure 3.** Evolution of craniofacial elongation in sexually dimorphic phenotypes in Apteronotidae. Stochastic character map summary of 1000 simulations showing the independent evolutionary transitions towards sexually dimorphic craniofacial elongation in the gymnotiform family Apteronotidae (93 spp.). Insets depict skulls of representative species from each clade. Stars denote species included in this study: *Apteronotus rostratus* (blue), *Compsaraia samueli* (black).

(*A. albifrons* clade and *A. leptorhynchus* clade) and up to six times within other apteronotid clades. Additionally, we find that the two focal species of this study (*A. rostratus* and *C. samueli*) independently evolved their respective patterns of secondary sexual dimorphism.
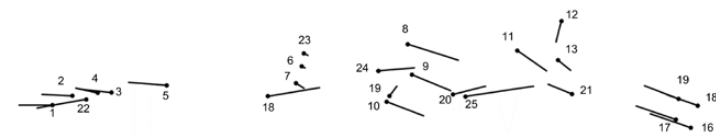
CRANIAL ALLOMETRY IN *APTERONOTUS ROSTRATUS*

The allometric deformations of male and female *A. rostratus* exhibit a common pattern seen across other electric fish species, where the facial region (LM 1–10, 18–19) expands, while the braincase (LM 11–17, 20–21) contracts relative to the face (i.e. heterocephaly; *sensu* Evans *et al.*, 2017b; Fig. 4). While this overall pattern is shared between the two sexes, other more localized differences are also apparent. Females exhibit less allometric facial expansion than males (evidenced by shorter vectors). Males also exhibit a more pronounced elongation of the posterior margin of the mandible encompassing the angular and retroarticular bones (LM 24 and 25).
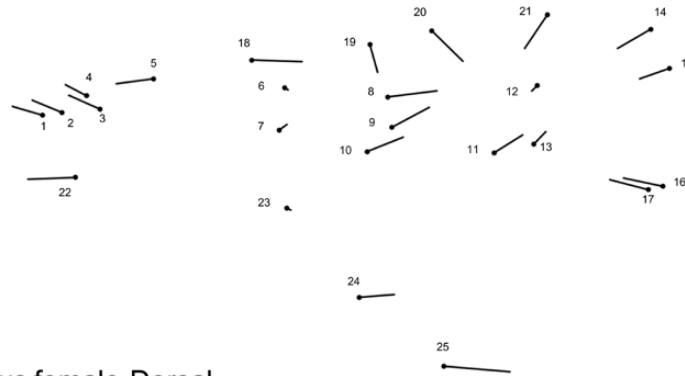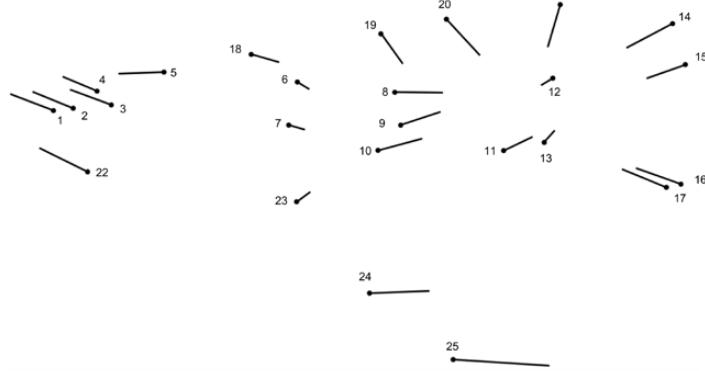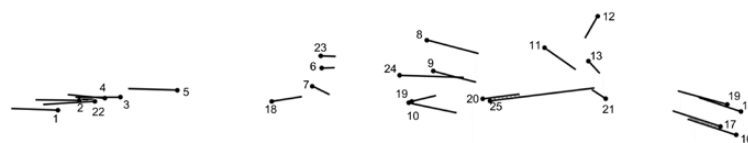


**Figure 4.** Allometric shape deformations for female and male *Apteronotus rostratus* specimens in lateral and dorsal views. Vectors indicate direction of landmark deformation from ball to stick.

CRANIAL ALLOMETRY IN *COMPSARAIA SAMUELI*

Differences in allometric deformation between male and female *C. samueli* are more pronounced than in *A. rostratus* (Fig. 5). Here, both males and females also exhibit heterocephaly. However, females exhibit a unique downward deflection of the facial region, while males exhibit an opposing and more common pattern in gymnotiform fishes in which the face extends both dorsally and anteriorly. In comparison to males, females exhibit a greatly reduced allometric contraction of the braincase, which results in a comparatively larger braincase in adult female specimens. Males and females also differ drastically in patterns of mandible growth. Here males elongate both the anterior and posterior regions of the mandible (LM 22, 24 and 25), while females, in contrast, exhibit relatively little change in mandible shape during growth.

STATIC ALLOMETRIC TRAJECTORIES IN *APTERONOTUS ROSTRATUS*

The allometric trajectories of male and female *A. rostratus* specimens exhibit significant differences. Size explains 56.2% of the total shape variance, while sex explains 1.6% (Table 2). A homogeneity of slopes test found a significant ($P = 0.002$) difference between allometric slopes, suggesting non-parallel slopes between the sexes. A Procrustes ANOVA found significant ($P = 0.020$) shape differences between males and females and a significant ($P = 0.006$) interaction
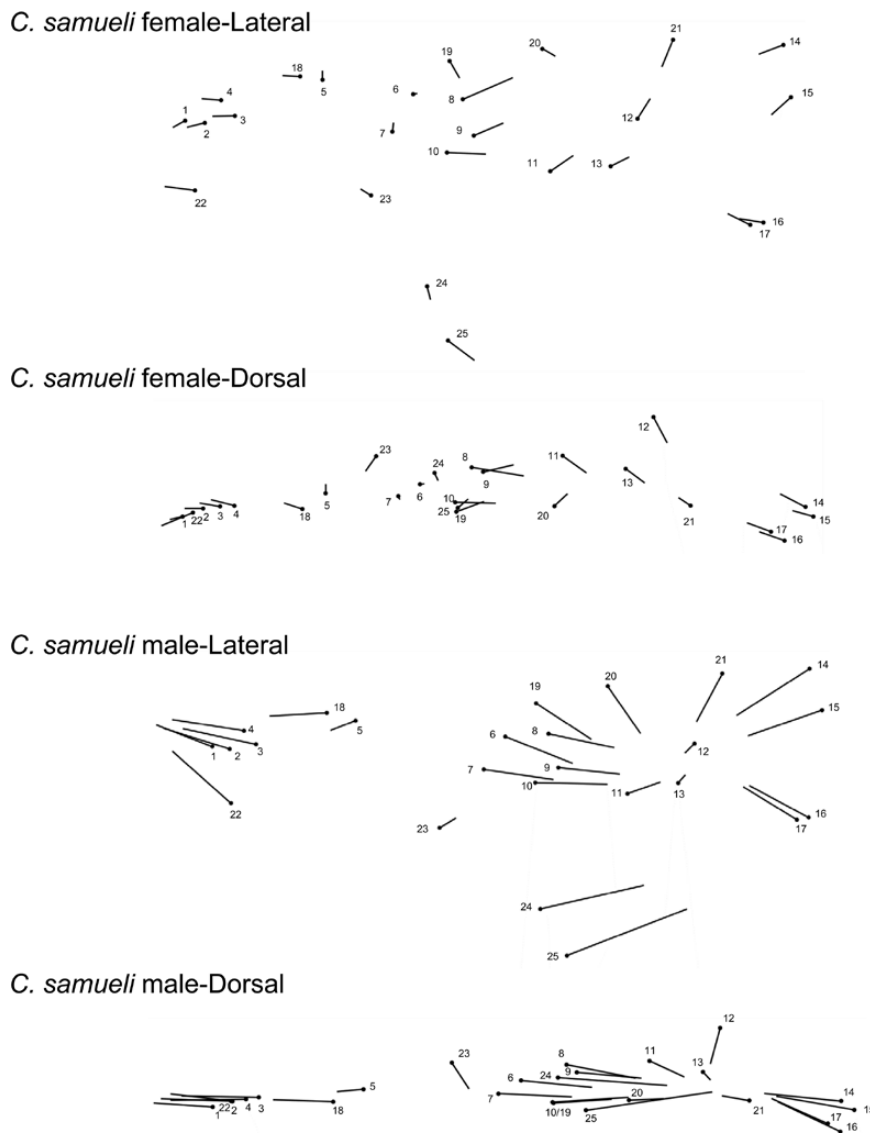


**Figure 5.** Allometric shape deformations for female and male *Compsaraia samueli* specimens in lateral and dorsal views. Graphical conventions as in Figure 4.

**Table 2.** Homogeneity of slopes test and Procrustes analysis of variance for ontogenetic trajectories of male and female *Apteronotus rostratus* and *Compsaraia samueli*. Bold values indicate statistical significance ($P < 0.05$)

Homogeneity of Slopes Test

| *A. rostratus* | Df | SSE | SS | R2 | F | Z | Pr(>F) |
|---|---|---|---|---|---|---|---|
| Common Allometry | 55 | 0.2161 | | | | | |
| Group Allometries | 53 | 0.1983 | 0.018 | 0.036 | 2.379 | 2.207 | **0.002** |
| | Df | SS | MS | Rsq | F | Z | Pr(>F) |
| log(size) | 1 | 0.277 | 0.277 | 0.562 | 74.038 | 19.548 | **0.001** |
| sex | 1 | 0.008 | 0.008 | 0.016 | 2.102 | 1.898 | **0.020** |
| log(size):sex | 1 | 0.010 | 0.010 | 0.020 | 2.451 | 2.464 | **0.006** |
| Residuals | 53 | 0.198 | 0.004 | | | | |
| Total | 56 | 0.493 | | | | | |

| *C. samueli* | Df | SSE | SS | R2 | F | Z | Pr(>F) |
|---|---|---|---|---|---|---|---|
| Common Allometry | 47 | 0.307 | | | | | |
| Group Allometries | 45 | 0.217 | 0.090 | 0.070 | 9.285 | 6.320 | **0.001** |
| | Df | SS | MS | Rsq | F | Z | Pr(>F) |
| log(size) | 1 | 0.977 | 0.977 | 0.761 | 202.485 | 17.428 | **0.001** |
| sex | 1 | 0.023 | 0.023 | 0.018 | 4.665 | 2.933 | **0.010** |
| log(size):sex | 1 | 0.067 | 0.067 | 0.052 | 13.905 | 9.359 | **0.001** |
| Residuals | 45 | 0.217 | 0.005 | | | | |
| Total | 48 | 1.284 | | | | | |

between size and sex. Males exhibit more positive allometric slopes than females, suggesting a faster rate of shape change relative to females (Fig. 6).

### STATIC ALLOMETRIC TRAJECTORIES IN *COMPSARAIA SAMUELI*

Allometric trajectories of male and female *C. samueli* also exhibit significant differences (Fig. 7). Size explains 76.1% of the total shape variance, while sex explains 1.8% (Table 2). A homogeneity of slopes test found a significant ($P = 0.001$) difference between allometric slopes, indicating non-parallel slopes between males and females. A Procrustes ANOVA found significant ($P = 0.010$) shape differences between males and females, and significant ($P = 0.001$) size differences. Similar to *A. rostratus*, male *C. samueli* also exhibit a more positive allometric slope than females, and experience a faster rate of shape-change relative to females.

### MECHANICAL ADVANTAGE IN *APTERONOTUS ROSTRATUS*

Mechanical advantage is negatively ($r = -0.48$) correlated with size in *A. rostratus* ($P < 0.001$) (Table 3; Fig. 8A). A significant relationship was found between lower jaw shape and MA ($P = 0.001$) (Fig. 9A). However, no significant ($P = 0.139$) interaction was found between MA and sex, indicating that males and females exhibit similar MA during growth (Table 4).

### MECHANICAL ADVANTAGE IN *COMPSARAIA SAMUELI*

Mechanical advantage was significantly ($P < 0.001$) correlated with size for both males and females of *C. samueli* (Table 3; Fig. 8B). Interestingly, males and females differ significantly ($P < 0.001$) in the allometric slopes of MA, where females exhibit a positive slope ($r = 0.53$), while males exhibit a negative slope ($r = -0.43$) (Table 3). A significant ($P = 0.001$), relationship was found between lower jaw shape and MA. Significant differences were also recovered between the sexes ($P = 0.005$). Here, females exhibit a positive slope ($r = 0.53$), while males exhibit a negative slope ($r = -0.43$) (Table 4; Fig. 9B). These results suggest that as males grow more elongate lower jaws, they sacrifice more efficient bite force transmissions.

### AGONISTIC INTERACTIONS IN *COMPSARAIA SAMUELI*

In the footage of male *C. samueli*, we observed several instances of agonistic interactions between males (Fig. 10A; Supporting Information, Movie S1). In these bouts, males were observed biting the heads, flanks and tails of other males. Additionally, males were observed locking jaws and pushing linearly with little or no twisting. Bouts were typically short (lasting around
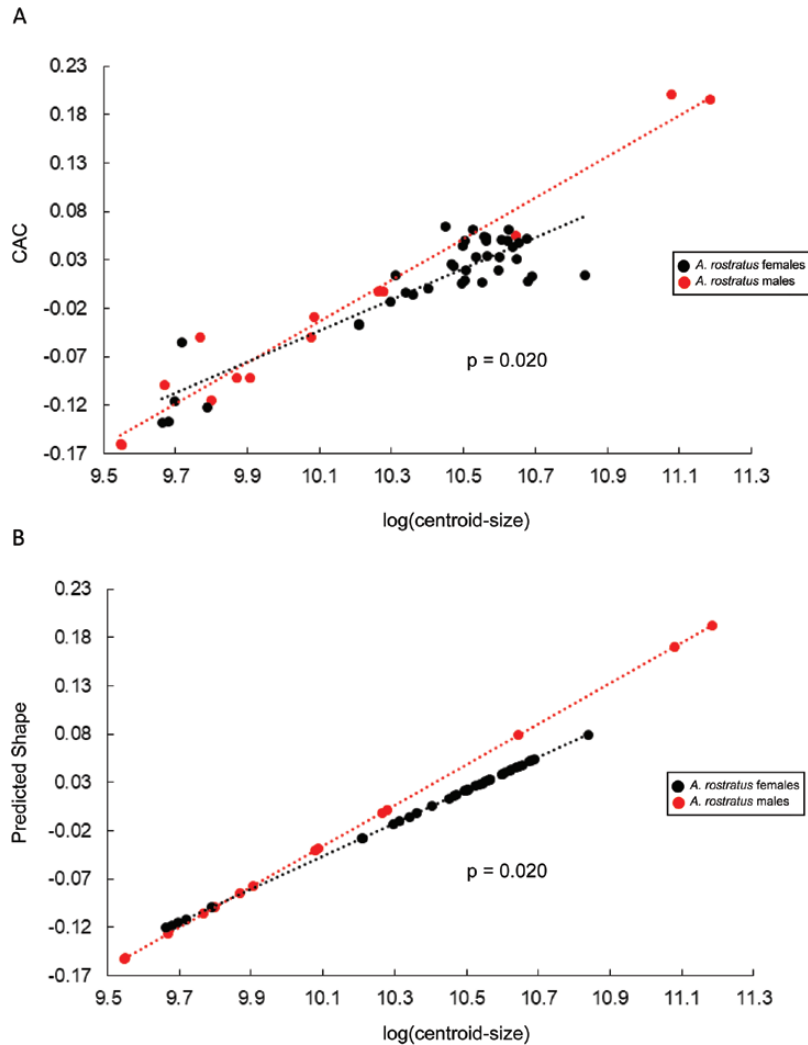
**Figure 6.** Allometric trajectories for male and female specimens of *Apteronotus rostratus* showing both common allometric components (A) and predicted shape (B).

two seconds) and never resulted in noticeable injuries to either participant. We also observed, for the first time in this species, a unique jaw-quivering behaviour, where males oscillate their lower jaws before and after engaging in physical contact. Additionally, we find that the jaws are used in an apparent display manner in which males open their jaws beyond 90° and face rival males without making physical contact (Fig. 10B).

## DISCUSSION

### POSITIVE ALLOMETRY IN THE SEXUAL WEAPONRY OF ELECTRIC FISHES

We find that both *A. rostratus* and *C. samueli* exhibit an independently evolved form of sexually dimorphic cranial elongation (Fig. 3). Interestingly, despite the independent origins of this phenotype, we recover a key

similarity between species in the developmental trajectories of sexually dimorphic males. Here, the underlying allometric trajectories that build the sexually dimorphic phenotypes of *A. rostratus* and *C. samueli* both exhibit more positive slopes in males relative to females. This suggests that males exhibit higher rates of shape change relative to size than do females. These findings are also consistent with the hypothesis that sexually selected traits evolve more positive slopes relative to non-sexually selected traits (Darwin, 1888; Gould, 1966, 1971; Andersson, 1994; Emlen & Nijhout, 2000).

### THE SCALING OF MECHANICAL ADVANTAGE DIFFERS AMONG SPECIES

Notable scaling differences in MA were observed among species. In *C. samueli*, jaw shape in males is negatively correlated with MA, while females exhibit
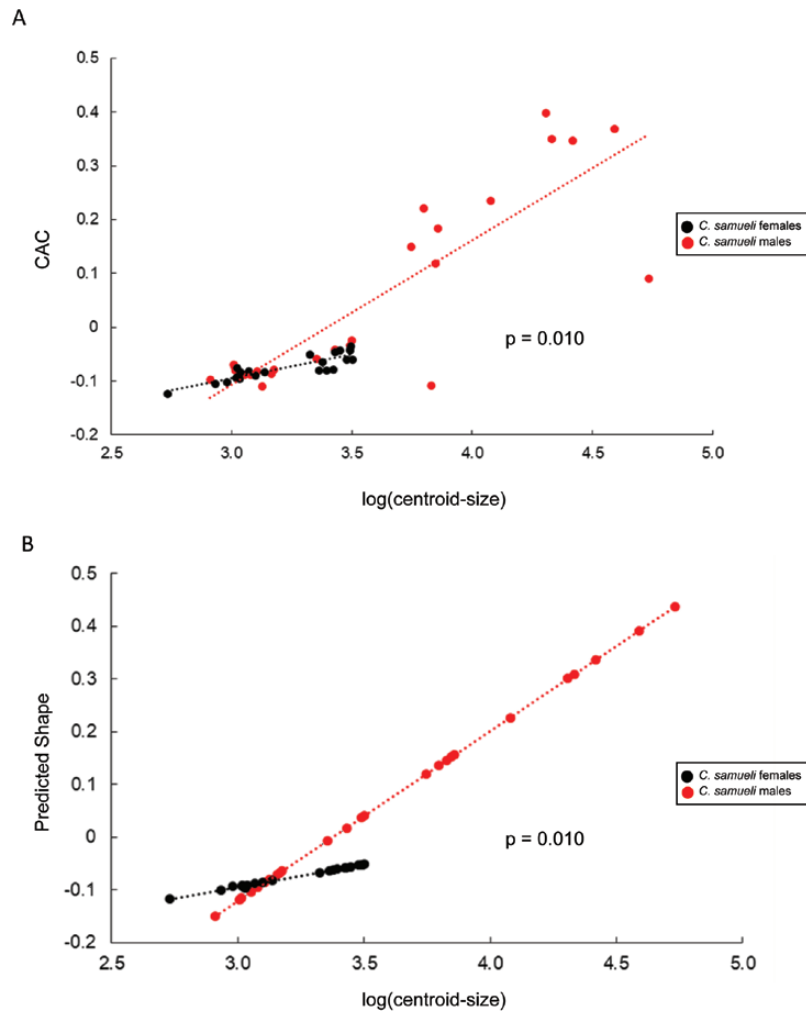
A



B

**Figure 7.** Allometric trajectories for female and male specimens of *Compsaraia samueli* showing both common allometric components (A) and predicted shape (B).

**Table 3.** Analysis of variance for the effect of log(centroid-size) and sex on mechanical advantage for *Apteronotus rostratus* and *Compsaraia samueli*. Bold values indicate statistical significance ($P < 0.05$)

| *A. rostratus* | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|---|---|---|---|---|---|
| size | 1 | 0.059 | 0.059 | 16.882 | **<0.001** |
| sex | 1 | 0.002 | 0.002 | 0.535 | 0.4677 |
| size:sex | 1 | 0.010 | 0.010 | 2.733 | 0.1042 |
| Residuals | 53 | 0.186 | 0.004 | | |

| *C. samueli* | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|---|---|---|---|---|---|
| size | 1 | 0.129 | 0.129 | 15.030 | **<0.001** |
| sex | 1 | 0.116 | 0.116 | 13.510 | **<0.001** |
| size:sex | 1 | 0.053 | 0.053 | 6.150 | **0.017** |
| Residuals | 45 | 0.385 | 0.009 | | |

an inverse pattern. This reduction in MA suggests that sexually dimorphic males have weaker jaw-closing forces than females (assuming similar muscle CSA and muscle insertion angles). This also suggests a performance trade-off, where males with elongate lower jaws sacrifice more forceful biting commensurate
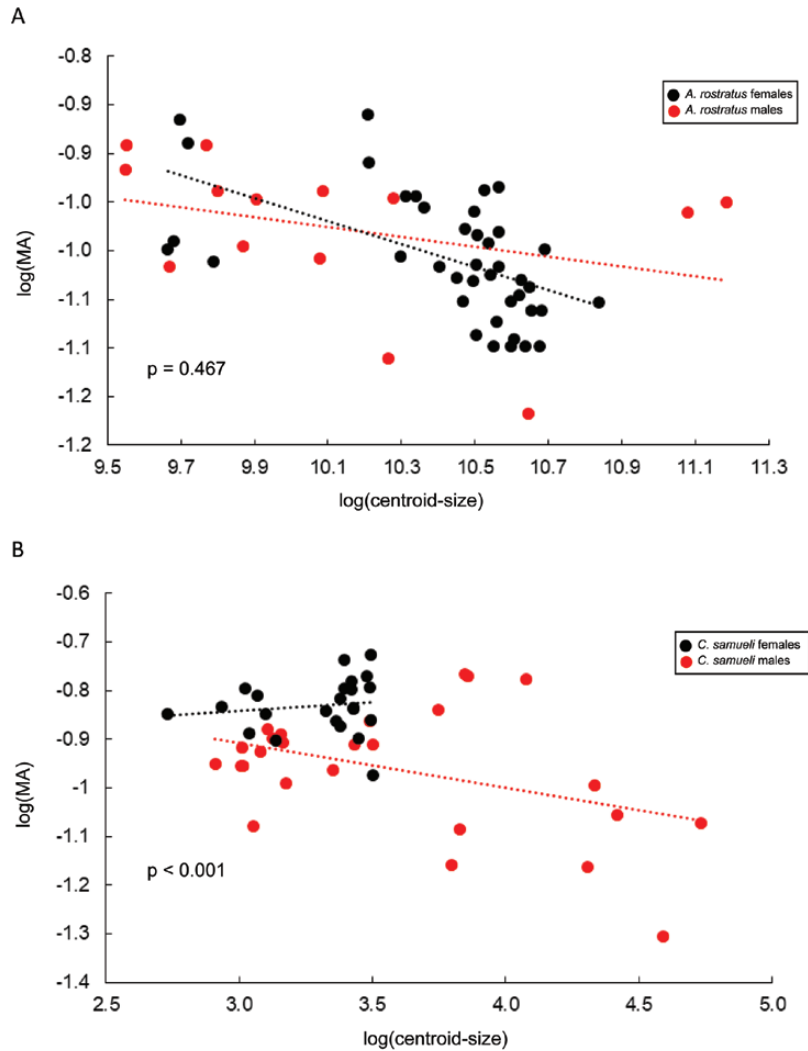
**Figure 8.** Allometric trajectories of lower jaw mechanical advantage (MA) in *Apteronotus rostratus* (A) and *Compsaraia samueli* (B).

with shorter jaws. This pattern is sharply contrasted with *A. rostratus,* which undergoes a reduction in MA with increasing body sizes, but exhibit no differences in MA between males and females. It is important to note that our estimation of jaw-closing performance assumes a constant muscle CSA between sexes, which may not necessarily reflect a biological reality. It is, therefore, possible that male *C. samueli* increase muscle CSA to compensate for decreases in MA. However, given the narrow, laterally compressed shape of these fishes, expansion of the jaw adductor musculature is not probable. It is also important to note that our performance model only considered mechanical advantage at the anterior-most tooth of the lower jaw; this model is potentially limited because it does not capture the full range of load application along the jaw. In some instances, when electric fishes lock jaws during combat, they bring almost the entire length of the jaw to bear. This suggests that the relative mechanical advantage at any (and every) point along the jaw is being realized. In order to more rigorously test this hypothesis, it will be necessary to incorporate muscle CSA and insertion angle to estimate bite forces between males and females, and model skull stresses during bending using finite element analysis *sensu* Rayfield (2007).

## WHY THE LONG FACE?

The snout of *Compsaraia* illustrates a common finding of many studies of animal weaponry: where the practical functions of an exaggerated weapon are greatly diminished, and the phenotype instead serves more as an assessment tool for other males to
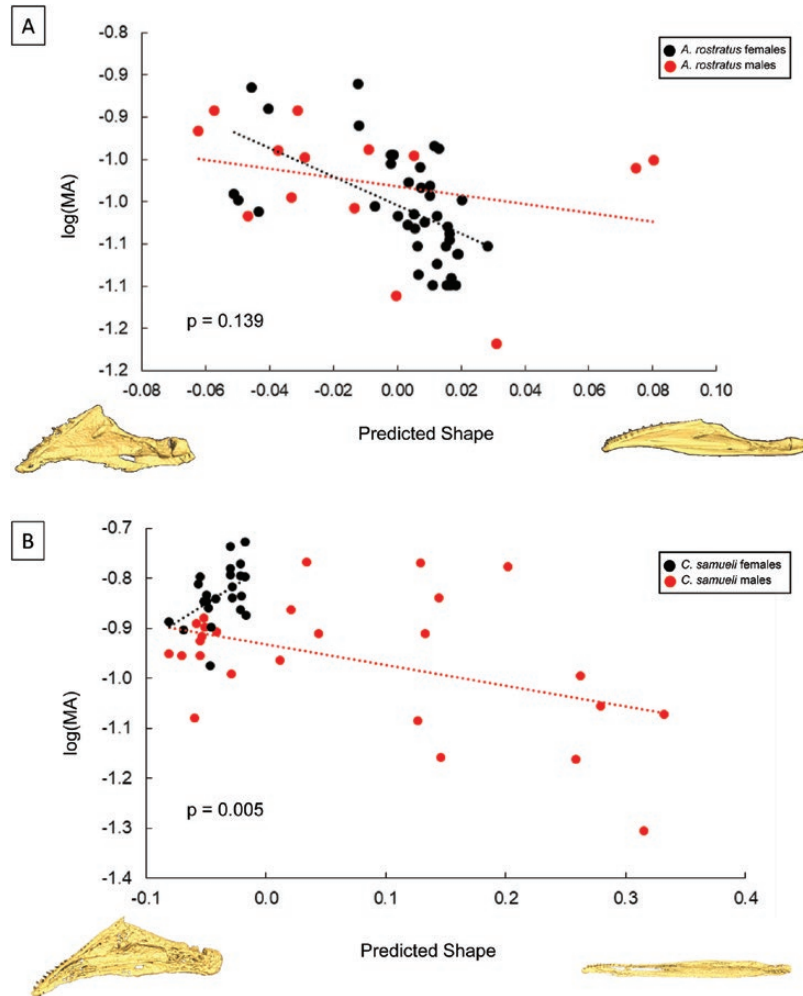
**Figure 9.** Scaling of lower jaw mechanical advantage and predicted jaw shape in *Apteronotus rostratus* (A) and *Compsaraia samueli* (B).

avoid serious conflict, and a signal in communication with potential mates (Arai & Sato, 2007; McCullough *et al.*, 2016). Support for the thesis that the rostrum of adult male *C. samueli* is functionally ceremonial rests on two lines of evidence: (1) the jaw's low mechanical advantage is not suitable for gripping or biting; and (2) the snout and jaws are poorly ossified and do not provide the structural rigidity needed for prolonged contests of strength, as compared to the more heavily ossified skulls of some other apteronotids (e.g. *A. rostratus*, Fig. 1). Even when sparring, *C. samueli* males face one another head-on, without any obvious rolling or twisting. Instead, males push each other linearly in contests analogous to sumo wrestling or tug-of-war, where opponents are pushed or pulled away from a central arena. Previous observations of *Apteronotus leptorhynchus* (a close relative of *A. rostratus*) indicate that males also engage in jaw

locking behaviors. However, unlike *C. samueli*, bouts between males were documented to last up to 15 minutes (Triefenbach & Zakon, 2008). Furthermore, *A. leptorhynchus* wrestling bouts include more twisting than they do in *C. samueli,* the latter of which are limited to pushing or pulling along the long axis of the body. This suggests that *C. samueli* utilize their elongate jaws more as a display or assessment tool rather than an actual weapon than is the case in *A. leptorhynchus* and *A. rostratus*, which engage in more prolonged and more physical bouts.

The elongate jaws of adult male *C. samueli* are like those of other elongate jaw-lever systems in being unsuitable for effective force transmission, i.e. less useful for fighting or feeding on hard or complex prey items (Porter & Motta, 2004; Habegger *et al.*, 2011; Goulet *et al.*, 2016). While reduced jaw leverage suggests that forceful biting or gripping are unlikely for

**Table 4.** Analysis of variance for the effect of jaw shape and sex on mechanical advantage for *Apteronotus rostratus* and *Compsaraia samueli*. Bold values indicate statistical significance ($P < 0.05$)

| *A. rostratus* | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
| --- | --- | --- | --- | --- | --- |
| shape | 1 | 0.051 | 0.003 | 14.472 | **0.001** |
| sex | 1 | 0.005 | 0.005 | 1.546 | 0.139 |
| shape:sex | 1 | 0.014 | 0.014 | 4.132 | **0.049** |
| Residuals | 45 | 0.238 | 0.004 | | |
| *C. samueli* | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
| shape | 1 | 0.196 | 0.196 | 22.799 | **<0.001** |
| sex | 1 | 0.074 | 0.074 | 8.645 | **0.005** |
| shape:sex | 1 | 0.028 | 0.028 | 3.250 | 0.097 |
| Residuals | 45 | 0.386 | 0.009 | | |
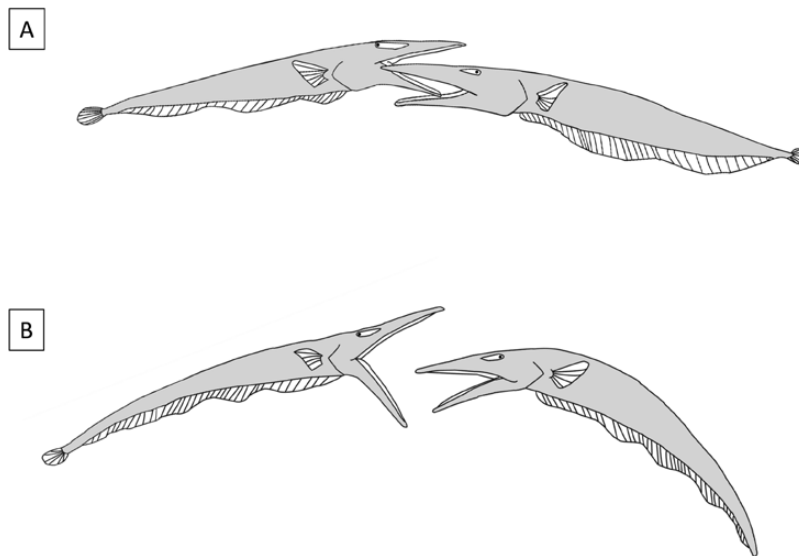


**Figure 10.** Observed agonistic interactions between male *Compsaraia samueli* specimens showing (A) jaw-locking and (B) mouth-gaping behaviours.

*C. samueli*, low mechanical advantage also results in faster jaw-closing (higher velocity transfer), which is useful for capturing elusive or cryptic prey (Ferry-Graham *et al.*, 2001). However, *Compsaraia* do not have the laterally constrained oral gapes or cranial kinesis typical of high-performance suction feeders like anabantids (gouramis), embiotocids (surf perch) or other gymnotiforms (Marrero & Winemiller, 1993), or more ram-suction feeders like tube-snouted syngnathids (pipefishes and seahorses), mormyrids (elephant fishes) and chaetodontids (butterfly fishes) (Ferry-Graham *et al.*, 2001; Roos *et al.*, 2011; Longo *et al.*, 2016). As such, the snout of *Compsaraia* is poorly suited for either biting, suction-feeding or even for picking through benthic invertebrate meiofauna (Marrero & Winemiller, 1993).

Selection pressures for elongate jaws in *C. samueli* could reflect a ritualized use of the structure, in which the oral jaws are more ornamental and less useful as a functional weapon. Larger, more exaggerated features are typical of high-quality males, and can serve to signal rivals that their competitor is robust, capable of defending a resource and not worth contesting (Emlen *et al.*, 2012; Dennenmoser & Christy, 2013; McCullough *et al.*, 2016). Some specimens of mature male *C. samueli* and *A. leptorhynchus* have been observed opening their jaws beyond 90º, presumably to display to rivals before and after physical contact. This 'mouth gaping' behaviour has been documented in other fish species (Ward, 1967; Dow *et al.*, 1976; Figler & Klauenberg, 1980; McFarland & Hillis, 1982; Summers *et al.*, 2004; Ritter, 2008) where it is thought

to serve a display/signalling function associated with agonistic interactions.

## CONCLUSION

The static allometric relationships that build the independently evolved sexual weaponry of *A. rostratus* and *C. samueli* both exhibit more positive slopes in males than in females, indicating that males undergo a faster rate of shape change during growth from juvenile to adults. Despite these similarities, we find that the performance consequences of facial elongation are not shared between these species. We find that male *C. samueli* experience a reduction in mechanical advantage (which differs significantly from females) as the lower oral jaw elongates, while male *A. rostratus* do not differ from females in mechanical advantage during growth. Differences in the mechanical advantage of the sexual weaponry between these two species suggests that these species utilize their jaws in slightly different ways during agonistic interactions and may reflect a functional gradient between armament and ornamentation that is seen across other taxa.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

**Table S1.** Materials examined for 106 specimens of *Apteronotus rostratus* and *Compsaraia samueli*.
**Movie S1.** Agonistic jaw-locking behaviour between two captive male *Compsaraia samueli* specimens.